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REVIEW

Fortifying crops with micronutrients for sustainable global nutritional security

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Abstract

The adverse effects of climate change on crop productivity and nutritional content have raised concerns toward food and nutritional security. These challenges can be mitigated by developing climate-resilient and biofortified crop varieties. A biofortification strategy focused on developing cultivars enriched in essential micronutrients is one of the most promising and effective approaches to addressing nutrient deficiencies in the context of a changing climate. Current efforts by scientists around the globe are aimed at bio-fortifying crops to meet present and future nutritional security needs. The grain fortification with enhanced mineral content in the seed endosperm/cotyledon depends on several factors: the nutritional status of the soil, the bioavailability of minerals in the rhizosphere, and, more specifically, the plant's ability to efficiently uptake and transport these nutrients to the sink organs. Microorganisms play a critical role in this process by improving soil health and facilitating the breakdown of trace elements through various biogeochemical cycles. In particular, plant growth-promoting (PGP) microbes, primarily actinomycetes, enhance bioavailability of minerals to crop plants, thereby improving seed mineral content. Emerging technologies and research innovations can combat global hidden hunger,

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Abbreviations: DM, dry matter; ETC, electron transport chain; GS, genomic selection; MTA, marker trait associations; OFSP, orange-fleshed sweet potato; SNP, single nucleotide polymorphism; PVE, phenotypic variance; QTL, quantitative trait loci; ROS, reactive oxygen species.

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and ensure nutritional security worldwide, even amidst the challenges posed by climate change. This review highlights the importance of biofortification, addresses the imminent challenges, and suggests actionable solutions. Additionally, it explores the combination of traditional agricultural practices with modern approaches to enhance nutritional quality of crops, thus contributing to a sustainable and secure food system for the future.

Plain Language Summary

The adverse effects of climate change on crop productivity and nutritional content have raised concerns toward food and nutritional security. These challenges can be mitigated by developing climate-resilient and biofortified crop varieties. A biofortification strategy focused on developing cultivars enriched in essential micronutrients is one of the most promising and effective approaches to addressing nutrient deficiencies in the context of a changing climate. Current efforts by scientists around the globe are aimed at bio-fortifying crops to meet present and future nutritional security needs.

1 | INTRODUCTION

Global climate change causes erratic rainfall, increased atmospheric CO_2 concentrations, and increased temperature, poses a significant threat to agricultural production, food security, supply chains, and human health, particularly through malnutrition (Srivastav et al., 2022). The global population could reach 8.5 billion by 2030, 9.7 billion by 2050, and 10.4 billion by the 2080s (Raghavan, 2025). The increasing population brings serious nutritional and food quality challenges (FAO, 2020). Population growth and dietary shifts are driving a dramatic increase in the demand for food. However, despite significant scientific advancements, a large portion of the population is still unable to access or cannot afford a nutritious diet, resulting in malnutrition and undernutrition (WHO, 2021). Malnutrition, particularly micronutrient deficiencies, remains serious concern, especially in developing countries, and is closely linked to climate change (FAO, 2018). Climate change adversely impacts the nutritional quality of crops by altering plant physiology and nutrient uptake. For instance, elevated atmospheric carbon dioxide (CO_2) levels increase carbohydrate accumulation in staple crops like wheat (*Triticum aestivum* L.) and rice (*Oryza sativa* L.), while simultaneously reducing their protein, zinc (Zn), and iron (Fe) concentrations, exacerbating nutrient deficiencies, particularly in developing regions (Myers et al., 2014). Furthermore, heat stress and erratic rainfall patterns negatively affect the level of vitamins in crops like tomatoes and leafy greens (Medek et al., 2017). These changes not only threaten global food security but also increase the risk of malnutrition, particularly for populations relying on staple crops for their essential nutrients intake (Smith & Myers, 2018). Malnutrition results from inadequate intake of essential nutrients and can manifest as both undernutrition and overnutrition. Overnutrition results from excessive consumption of calories and nutrients and has also become a growing concern (Shahzad et al., 2021). Malnutrition has severe socioeconomic repercussions, particularly in developing and underdeveloped nations where people consume an unbalanced diet. Micronutrients deficiencies remain an important global public health issue, especially in regions with limited access to diverse diets (Ebbisa, 2022). Globally, over 821 million people are undernourished, 2 billion suffer from micronutrient malnutrition, and another 2 billion are overweight or obese (FAO, 2021; Koc & Karayigit, 2021; Sheoran et al., 2022). These micronutrient deficiencies impact individuals across all age groups (Pumariega et al., 2022).

Micronutrients, required in minimal amounts (100 mg daily), are essential for overall growth and disease prevention. Micronutrient deficiency, often referred to as "hidden hunger," results from the dietary lack of essential vitamins and minerals (Joshi et al., 2022; Koc & Karayigit, 2021). This deficiency leads to diseases, immune system disorders, and a decline in physical growth and mental development. Malnutrition causes up to 45% of child mortality (5 years); 151 million children (22%) are stunted, and 51 million (7%) are underweight for their height (X. Li et al., 2022). Despite consuming a carbohydrate- and protein-rich diet, hidden hunger persists due to insufficient micronutrient intake.

South Asia, in particular, faces an alarming situation of malnutrition, with 88% of Asian and African nations simultaneously confronting two or three types of malnutrition, such as undernutrition, micronutrient deficiencies, and obesity. In South Asia, malnutrition is rising due to inadequate food supply, low family income, inadequate healthcare infrastructure, and poor childcare practices (Akhtar, 2016). The region has 33.3% of children (5-year-old) moderately or severely stunted, 15.3% wasting (low weight for their height), and 3.1% overweight (Ngonga, 2022). Despite progress in several WHO nutrition indices, the South Asian region remains far from reaching its nutrition targets. Particularly concerning is the 40%–50% of women of reproductive age who suffer from anemia, which is linked to malnutrition in children. South Asian countries have the highest child malnutrition frequency, affecting their economic development (Akhtar et al., 2013; S. B. Kumar et al., 2022; Lele et al., 2016; Shekari et al., 2015). Both nutrient and vitamin deficiency are major contributors to global malnutrition. Vitamin A deficiency is a chronic public health concern in developing countries, where economic insecurity, poor diet, and inefficient food distribution exacerbate the issue (S. B. Kumar et al., 2022). About 254 million children are vitamin A deficient, and 2 billion individuals globally suffer from iodine (I) deficiency (S. B. Kumar et al., 2022). Surveys reveal that 5.2 million preschool-aged children suffer from night blindness, and 190 million have low blood retinol levels due to vitamin A deficiency. The highest rates of vitamin A deficiency were found in South Asia and Sub-Saharan Africa (Esio-Bassey, 2022). Additionally, approximately 30% of the global population is affected by anemia (S. B. Kumar et al., 2022), with the highest prevalence observed in developing countries, especially in Africa and Southeast Asia (Natekar et al., 2022). Conversely, overnutrition is also rising, leading to overweight issues and obesity-related health problems (M. K. Khan et al., 2022). Given these challenges, biofortification is a key approach for addressing nutrient deficiencies, while also promoting sustainable agricultural practices.

Recent advancements in agriculture are focused on developing high-yielding and nutrient-rich crops. Biofortified crops are developed to have essential micronutrients, providing a cost-effective, long-term solution to combat hidden hunger. Once biofortified crops are developed, they incur no additional costs associated with fortifying food products during processing. In agriculture, strategies such as selective fertilizer use, crop breeding, and genetic modifications are used to increase the micronutrient levels in crops (Monroy-Gomez et al., 2022). Biofortification has already proven to be an effective intervention in improving crop nutritional content and combating malnutrition (Garg et al., 2018). Biofortification enhances the nutrient content of crops by increasing essential vitamins and minerals, thereby improving the nutritional profile of staple foods and supporting overall health while addressing deficiencies. The consumption of biofortified crops significantly increases nutrient intake, making it a key approach against global malnutrition (Buturi et al., 2022; Rehman et al., 2021). This review highlights the role of biofortification in mitigating the impacts of climate change on food and nutrition security and discusses various biofortification strategies, including agronomic practices, conventional breeding, and molecular and genetic approaches. It also outlines current efforts and future prospects for improving crop nutritional value.

Climate change impacts plant physiological and developmental processes, as well as molecular functions, morphological traits, and biochemical characteristics (Gray & Brady, 2016). Understanding its impact on food and nutritional security is essential, as it emphasizes the need to develop nutrient-enriched, high-yielding biofortified crops to address the challenges posed by future climate scenarios.

Core Ideas

- Global climate change is a global concern, and it has huge impact on nutritional security worldwide.
- Climate and environmental stress have greatly impacted global food productivity and nutritional content.
- Genomic approaches have made huge contribution toward developing climate-smart crops.
- Molecular breeding and identification of QTLs for Fe-Zn content.
- Genome editing and the Clustered Regularly Interspaced Short Palindromic Repeats (CRISPR)/Cas system emerged as key tools for developing climate-smart bio-fortified crop plants.

2 | NEED AND IMPORTANCE OF BIOFORTIFICATION

Billions of smallholder farmers, who produce one-third of the world's food supply and primarily depend on staple crops, face a direct nutritional threat from global warming. In low-income countries, agriculture is the primary source of nutrition and income (S. B. Kumar et al., 2022). However, the diet in these regions is often deficient in essential nutrients, such as vitamin A, iron (Fe), zinc (Zn), calcium (Ca), manganese (Mn), copper (Cu), iodine (I), and selenium (Se). To ensure proper health, humans need approximately 40 recognized nutrients in adequate amounts. These include mineral elements like sodium (Na), potassium (K), calcium (Ca), magnesium (Mg), phosphorus (P), chlorine (Cl), and sulfur (S), which are considered as essential nutrients but are needed only in trace amounts. Micronutrients include Fe, Zn, Cu, Mn, I, Se, molybdenum (Mo), cobalt (Co), nickel (Ni), and vitamins. These nutrients are critical for physical and mental development and various metabolic processes. Micronutrient deficiency levels in crop plants range from 1 to 5 for Cu, 10 to 20 for Mn, 15 to 20 for Zn, and 50 to 100 for Fe (mg kg^{-1} dry matter [DM]) (P. Sharma et al., 2021). Various micronutrients function as cofactors for biological enzymes that control essential metabolic processes (Rodriguez-Cano et al., 2020). Among the most common micronutrient deficiencies, Fe and Zn are critical (Srungarapu et al., 2022). Fe is important for functions such as electron transport chain (ETC), DNA synthesis, and oxygen transport. Fe deficiency causes anemia, which impairs immune function, cognitive development, and physical capacity (Naveed et al., 2020). Similarly, Zn, the second most abundant transition metal in the human body, is needed for the normal function of various essential proteins, notably transcription factors and enzymes (Jomova et al., 2022). Additionally, Zn plays a vital function in antiviral immunity, and its supplementation was recently recommended for COVID-19 treatment (Ahmed et al., 2021). Iodine deficiency, on the other hand, leads to severe health issues like cretinism, goiter, stillbirth, thyroid inflammation, and cognitive impairment (Koc & Karayigit, 2021). Deficiencies in Zn, Fe, I, and vitamin A contribute to 20% of deaths of children under age five (Tam et al., 2020). Additionally, Fe, vitamin B_{12}, and vitamin A deficiencies affect 24.8% of the global population (FAO, 2020; Koc & Karayigit, 2021), while Se deficiency, particularly prevalent in China, Africa, and Northern Europe, affects 0.5–1 billion people worldwide. Se prevents "Keshan disease," a fatal cardiomyopathy disorder (Liao et al., 2024).

Micronutrient deficiencies in soil are closely linked to various environmental factors. Soil pH plays a crucial role in determining nutrient availability, microbial activity, and overall crop development (Song et al., 2019). Temperature and precipitation influence soil pH, while leaching and mineral weathering impact the nutrient supply. Generally, as soil pH increases, the availability of most micronutrients, except molybdenum (Mo), decreases. For example, Zn deficiency is often a result of high pH, excessive calcium carbonate ($CaCO_3$), low organic matter, poor soil moisture, and flooding-induced electrochemical changes (Thapa et al., 2021). Mn deficiency is commonly observed in silica-rich, calcareous sandy soils with neutral to alkaline pH (Alloway, 2009). As pH increases, the solubility of free iron (Fe) decreases by 1000-fold, significantly reducing its availability in alkaline and calcareous soils (pH > 7), which is a widespread issue in arid regions (FAO, 2016). Environmental factors like soil moisture, temperature, and soil type influence micronutrient uptake. For example, low temperatures and humidity reduce micronutrient availability, dissolution rates, root activity, and nutrient diffusion in the soil (Bhattacharya, 2021). High temperatures disrupt root function, impairing nutrient transport, reduce Fe uptake by promoting phytosiderophore's microbial decomposition and increase CO_2 production, and lead to increased soil leaching and nutrient loss (Gong et al., 2021; Marschner et al., 2011). Low soil temperature also inhibits phytosiderophore production and soil Fe mobilization, reducing uptake by gramineae species.

Several approaches have been suggested to address micronutrient deficiencies, including food fortification, micronutrient supplementation, and dietary diversification. However, developing nutrient-rich crops through agronomic or genetic approaches offers a more feasible way to reach individuals with limited access to fortified foods (P. Sharma et al., 2017). Biofortification focuses on enhancing the nutrient content of staple foods consumed by poor households, requiring a one-time investment in developing fortified crops. Biofortification enhances micronutrient content of crop, addressing nutritional challenges linked to climate change and improving food security. By enhancing essential vitamins and minerals, biofortified crops may indirectly support plant stress tolerance, strengthening plant metabolic functions and resilience in crops (Maqbool et al., 2020). This approach not only improves food security and productivity but also stabilizes crop yields and nutrition.

3 | AGRONOMIC BIOFORTIFICATION STRATEGIES: UTILIZING FERTILIZERS

Several biofortification approaches have been adopted so far to combat the global challenges of malnutrition and food security (Figure 1). Agronomic biofortification involves the application of micronutrient fertilizers to the soil or directly to the plant to increase the concentration of these elements in the edible parts of a plant (Saltzman et al., 2017). This method provides a temporary increase in the micronutrient levels in the productive parts of plants. However, the efficiency of agronomic biofortification relies on factors such as soil type, nutrient accumulation, and mineral mobility. Although this approach is cost-effective, it is time-consuming and requires continual micronutrient supplementation. It primarily focuses on utilizing mineral fertilizers, notably Fe and Zn, to improve their solubility and mineral concentration in the soil (Garg et al., 2018; S. B. Kumar et al., 2022; Sheoran et al., 2022; Srivastav et al., 2022). These essential nutrients are supplied externally to the plant during various developmental stages. On the other hand, foliar fertilization enhances the nutrient content in grain and other plant parts via leaves. Strategic use of agronomic biofortification can also address environmental challenges. The effectiveness of this approach mainly depends on effective management practices. By applying fertilizers strategically, crop yields can be increased, thereby enhancing land productivity. This tackles the increasing worldwide demand for food without requiring deforestation or the transformation of natural ecosystems into agricultural land. By enhancing agricultural productivity on existing land through the use of fertilizers, the need to transform forests and other natural ecosystems into cropland is reduced. This contributes to conservation of biodiversity and the maintenance of critical ecosystem functions.

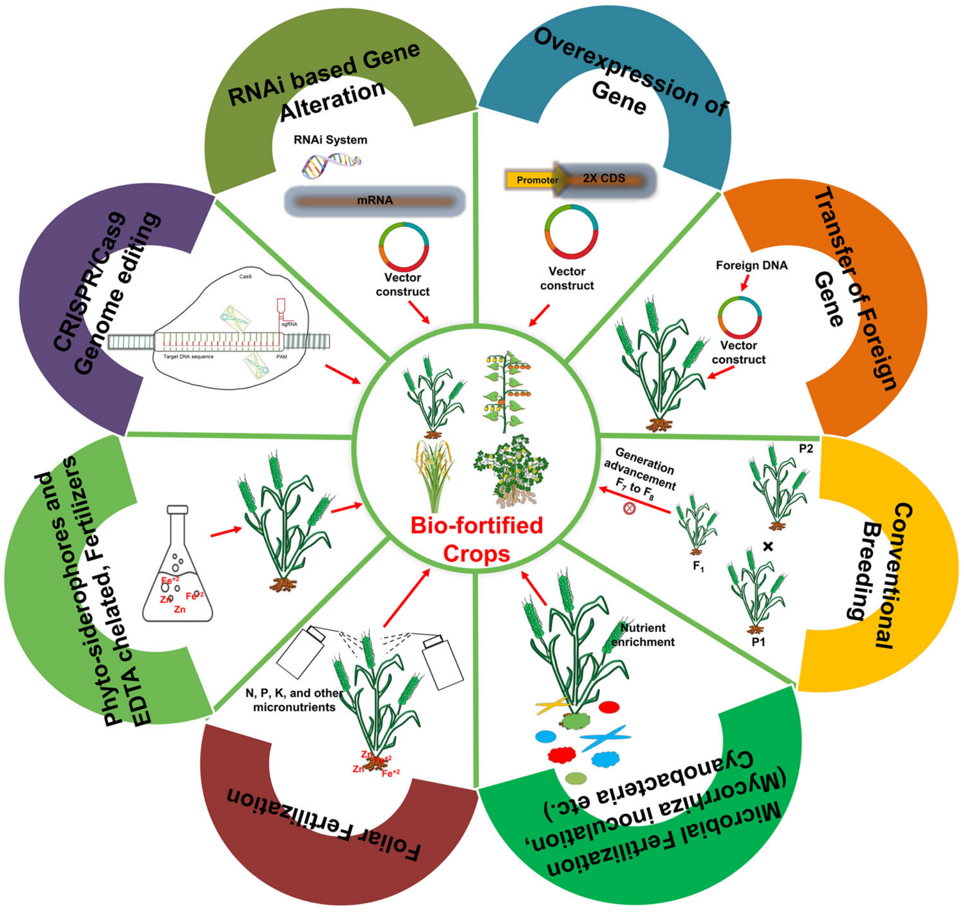

FIGURE 1 Illustration of various biofortification approaches for enhancement of micronutrient content.

Advanced technology in precision agriculture now enables farmers to apply fertilizers with precise accuracy, considering the specific needs of each crop. This reduces excessive use of fertilizers and minimizes their environmental consequences, especially by limiting nutrients runoff. Applying fertilizer technologies with precision is now a crucial advancement for sustainable agriculture. This approach boosts crop yields and nutritional content while making the most of resources and minimizing environmental harm. Precision agriculture, leveraging advanced sensors, remote sensing, and artificial intelligence (AI), further refines fertilizer management (Xing & Wang, 2024). Integrating these technologies with tailored farming methods and detailed tracking is essential for enhancing nutrient cycling and maintaining healthy soils.

Additionally, controlled agricultural systems that incorporate targeted fertilizer application can also contribute to carbon sequestration in soils. By capturing atmospheric carbon dioxide and storing it in the soil, this practice can help mitigate the impacts of climate change. When fertilizers are applied carefully and deliberately as per the crop requirement, they can enhance nutrient content as per the crop requirement because crops like legumes and cereals have differential demand for NPK during their vegetative growth, flowering time, and seed-filling stages. Further, a healthy soil can effectively retain water, minimize erosion, and promote diverse microbial communities, thereby strengthening ecosystem's resilience. Therefore, ensuring food security in the future requires the appropriate application of fertilizer. The fertilizer industry's 4R Nutrient Stewardship standards (Johnston & Bruulsema, 2014) provide a global framework for best management practices in fertilizer use, aiming to balance social, environmental, and economic goals. Although the scientific basis of the 4Rs is universal, their practical application is highly dependent on local context, adapting to specific agricultural systems, socio-economic realities, and biophysical environments. Recently, researcher Nigon (2024) suggested the 4R measures can differ according to the geography, soil health, and economics and development status of countries. For instance, in sub-Saharan Africa, 4R initiatives may focus on empowering farmers with better fertilizer practices, providing regional guidance for balanced nutrient application, and educating them on optimal timing and placement for cost-effective and efficient use. While in India, promoting site-specific fertilizer recommendations and supportive regulations for balanced nutrient use are key to maximizing the impact of the 4Rs. Developed nations like the United

States can further refine 4R implementation through advancements in precision nutrient management technology. Some important published outcome were reviewed by Zhu et al. (2025) and Tian et al. (2024), which suggest deep placement of nitrogen fertilizer while fertilizing crops enhances N use efficiency (N is available for longer duration as it does not get washed away by water) and reduces greenhouse gas emissions, which leads to reduced application of N fertilizer and enhances the overall crop productivity. Likewise, incorporating controlled-release fertilizers into soil gradually releases nitrogen (N) over approximately 50–110 days (Ransom et al., 2020). Further, across the globe, a focus on innovation in soil and water conservation is essential to improve nutrient and water-use efficiency as droughts become more frequent. Moreover, emerging scientific innovations, such as high-resolution geospatial mapping, improved weather forecasting, soil moisture measurement tools, rapid spectroscopy-based soil testing, fertilizer nanotechnology, and bio-stimulants (Nigon, 2024), hold promise for increasing crop yields and enhancing fertilizer efficiency.

Moreover, to maximize the benefits of agronomic fertilizers while minimizing environmental damage, it is crucial to adopt sustainable and responsible agricultural practices. Continuous research and innovation in agricultural practices are crucial for advancing and promoting environmentally sustainable fertilization processes. Fertilizers used in agronomic biofortification can be further classified into the following categories:

3.1 | Mineral fertilizers

Micronutrient-enriched fertilizers are one of the most cost-effective and direct biofortification approach. In regions suffering from micronutrient deficiencies, applying fertilizer supplemented with micronutrients to soil and leaves has shown increased micronutrient concentration and yield (Garg et al., 2018; Sheoran et al., 2022). Application of Fe and Zn fertilizer can enhance both yield and accumulation of micronutrient content in cereal crops like rice, wheat, and maize (*Zea mays* L.) (Alloway, 2009; Cakmak et al., 2010). As Zn plays a key role in boosting the human immune system, developing wheat and rice cultivars with a higher Zn concentration may have beneficial health impacts. The application of $ZnSO_4 \cdot 7H_2O$ (21% Zn) at 62.5 kg ha^{-1} or $ZnSO_4 \cdot H_2O$ (33% Zn) at 40 kg ha^{-1} has proven effective and cost-effective in addressing Zn deficiency in various crops. Nitrogen-fixing plants such as broad bean, vetch, and clover, along with the use of Zn-coated urea fertilizer, also increase the concentration of Zn in grains and straw. Notably, application of Zn-supplemented urea improved Zn absorption, crop productivity, and the quality traits of basmati rice more effectively than traditional fertilization with $ZnSO_4$ (Cakmak et al., 2010). Similarly, in soybean (*Glycine max*), applying Se and Zn fertilizers enhances the concentration of Se and Zn in the seeds, subsequently improving their physiological status (Jha & Warkentin, 2020). Applying micronutrients through soil surface fertilization is proven adaptive and effective technique to address boron deficiency (Koc & Karayigit, 2021). However, various anthropogenic activities, such as transportation, mining, pesticide usage, sludge reuse, and wastewater irrigation, contribute to heavy metal contamination in arable soils (Garg et al., 2018; Koc & Karayigit, 2021; Srivastav et al., 2022). As a result, the heavy metal accumulation alters soil ecology and poses significant risks to human health (X. Li et al., 2022). Furthermore, the usage of manure and inorganic fertilizers may also lead to the accumulation of heavy metals in the soil (Garg et al., 2018). Cadmium (Cd), being highly mobile in soil and plants, is one of most toxic heavy metal for humans. However, Zn can compete with Cd for the membrane transporters in plants, thereby reducing absorption and minimizing oxidative damage. The application of Zn at suitable concentrations in cereals grown in high Cd-soils reduces Cd absorption and accumulation (Shahzad et al., 2021). Other elements, such as Fe and Mn, also play a role in limiting Cd uptake by roots through competition for membrane transporters. These elements protect against damage to the plasma membrane by reducing reactive oxygen species (ROS) (Sheoran et al., 2022; Srivastav et al., 2022). A deficiency of Fe can accelerate Cd deposition, so adding Fe to Cd-contaminated soils can raise the Fe concentration while decreasing Cd uptake in crop plants. Although inorganic Fe fertilizers oxidize and precipitate into plant-unavailable forms, the use of Fe chelates and soil acidification can improve Fe uptake and availability (Garg et al., 2018; Sheoran et al., 2022). In addition to increasing the concentration of micronutrients with mineral fertilizers, recycling micronutrients is crucial due to rising fertilizer costs and environmental concerns.

3.2 | Foliar sprays

While soil fertilization can enhance the concentration of certain micronutrients in grains, it has limitations, especially for immobile minerals like Fe, which quickly transforms into insoluble Fe^{3+} in the soil, making it unavailable to plants. Foliar application of fertilizer addresses these challenges by spraying micronutrient solutions directly onto leaves, allowing absorption through stomata and epidermis. Foliar application of fertilizers has been shown to be more effective than soil fertilization in terms of nutrients utilization and in mitigating visual and soil deficiency issues. Several studies reported the effectiveness of foliar application of mineral fertilizers to various crops. Foliar application of Se during seed soaking or during wheat growth phase has been found to enhance Se content in wheat grains (Masarovicova & Kralova, 2012). Similarly, foliar application of Zn also enhances the concentration of Zn in edible parts of the plants (Saltzman et al., 2017). In wheat, foliar applications of 0.5% Zn and Fe at various growth stages increased Zn (17.3%–38.8%) and Fe (13.1%–30.3%) concentration, and also enhanced grain yield by 2.5%–5.1% (Al Noor et al., 2019). Similarly, in rice, foliar application of Zn and Fe at different growth stages increased grain Zn (30.8%–44.8%) and Fe (22%–38.2%) concentrations, and increased grain yield by 6%–10.3% (Gregorio et al., 2000). Foliar application of Cu at 60 and 90 DAS enhanced Cu concentration and crude protein production in fodder oats (Saltzman et al., 2017), while in cowpea, soil fertilization followed by foliar Zn fertilization provided better yield and nutritional content compared to foliar application alone (Pray & Listman, 2006).

Additionally, foliar application of Zn and Mn enhanced crop production in rice, wheat, and barley (*Hordeum vulgare* L.) (Kumari et al., 2020). To address I deficiency, surface applications of KIO_3 have been shown to increase I concentration in wheat, maize, and rice (Cakmak et al., 2010; Lyons et al., 2004).

3.3 | Microbial biofertilizers

Soil microorganisms, often referred to as the “invisible engineers” of the soil (Gadd, 2010), play a role in improving micronutrient uptake by plants. Plant growth promoting microbes, like fungi, bacteria, actinomycetes, cyanobacteria, and mycorrhizae, promote micronutrient absorption through phytohormones production, micronutrients solubilization, nitrogen fixation, and chelation (Rana et al., 2020; Yadav, 2020). Biofertilizers, which are microbial inoculum added to the soil, promote plant growth by improving nutrient acquisition (D. Bhardwaj et al., 2014; Sahoo et al., 2013). Naturally existing soil microorganisms, notably bacteria and mycorrhizal fungi, have emerged as a viable micronutrient enhancement method for major crops (Dhiman et al., 2023). In contrast to chemical fertilizers, biofertilizers limit environmental pollution, are cost-effective, and promote sustainable agriculture (Garg et al., 2018; Kaur et al., 2020). Zn, the second-most abundant metal in living organisms after Fe, is involved in several vital processes, including nucleic acid synthesis, lipid and protein production, and auxin regulation. Zn deficiency arise mainly because plants cannot absorb soil-based zinc. Microbial biofortification can be employed as an approach to improve Zn deficiency (Dotaniya et al., 2016). Zn biofortification using cyanobacteria (*Azotobacter* sp. and *Anabaena* sp.) and *Bacillus aryabhattai* has been reported in maize (Prasanna et al., 2015), soybean (A. Ramesh et al., 2014), and wheat (A. Ramesh et al., 2014). The soil microbes and plants maintain a symbiotic relationship. Mycorrhiza inoculation is recognized as a feasible alternative for increasing production without contaminating soil and water or disturbing the ecosystem. Mycorrhizal fungi, particularly arbuscular mycorrhizal fungi (AMF), often used as biofertilizers that promote micronutrient uptake and improve water efficiency. Inoculation of AMF (*Rhizophagus irregularis*) increases plant dry matter and primary metabolites, such as amino acids, sugar, fatty acids, secondary metabolites like polyphenols, and minerals such as K, Ca, P, Cu, Mg, Fe, Na, Zn, and Mn in some medicinal plants like *Mentha pulegium* and *Petroselinum Hortense* (Gashgari et al., 2020) (Table 1). AMF inoculation improves soil-applied Zn absorption and mobilizes micronutrients in wheat and barley (Coccina et al., 2019), while *Pseudomonas chlororaphis*, isolated from maize, promotes Fe uptake, germination, plant development, and grain yield (A. Sharma et al., 2003). Several microbes exude siderophores, which are Fe-chelating compounds that improve the absorption of micronutrients like Fe. Positive associations between rice yield, quality parameters, and soil microbiological parameters emphasize the importance of micronutrients uptake and mobilization by soil microbes. Table 1 lists some of the key components of major crops together with their important results.

3.4 | Nano-fertilizers

Nanotechnology has emerged as a promising innovation in agriculture through the development of nano-fertilizers, which are micronutrient-loaded particles developed to improve nutrient use efficiency and crop productivity. Nanoparticles, due to their small size and relative mobility interact more effectively with plant cells, improving nutrient uptake (Babu et al., 2022). The use of nanotechnology and biotechnology can enhance crop productivity, improve food nutrition, and increase fertilizer-micronutrient use efficiency (Koc & Karayigit, 2021). New techniques like nano-encapsulation, nano-materials, nano-devices, and nanoparticles aim to enhance micronutrient utilization efficiency (Monreal et al., 2016). Micronutrients are encapsulated in nanoscale materials and coatings by nano-encapsulation and products are called nano-fertilizers (A. K. Bhardwaj et al., 2022). Submicron nano-capsules encapsulate nanometric films, layers, and coatings, which transfer nutrients directly to the site of action. Microcapsules, nano-capsules, nano-materials, and nanoparticles containing micronutrients, including Zn, Fe, Mn, and CuO, boost crop production and micronutrient concentration. Encapsulation protects micronutrients from environmental factors such as pH, light, and oxidants. Encapsulation increases the solubility of less soluble substances to enhance micronutrient bioavailability (Monreal et al., 2016). Belal and El-Ramady (2016), revealed that coating nutrients in water-soluble fertilizers with resin-polymer, wax, and sulfur minimizes nutrient loss by controlled release,

TABLE 1 Use of beneficial microflora for enhancement of micronutrient's uptake in cereals and legumes.

Crop	Target element	Strains	Significant outcomes	References
Chickpea	Fe, Zn, Ca, Cu, Mn, and Mg	*Streptomyces*	Actinobacteria isolates increased the content of Iron (10%–38%), zinc (13%–30%), calcium (14%–26%), copper (11%–54%), manganese (18%–35%), and magnesium (14%–21%).	(A. Sharma et al., 2003)
Rice	Zn	*Ralstoniapicketti*	Isolate Zn 3 (62.48 mg/L) showed greater solubility of Zinc in broth culture.	(Gontia-Mishra et al., 2017)
Chickpea and Pigeonpea	Ca, Cu, Fe, Zn, and Mn,	*Pseudomonas plecoglossicida*, *Bembidion antiquum*, *Acinetobacter tandoii*, *Enterobacter ludwigii*, and *Pseudomonas monteilii*	Both chickpea (*Cicer arietinum* L.) and pigeonpea (*Cajanus cajan*) have increased mineral content, including iron (18%), zinc (23%), copper (8%), manganese (2%), calcium (22%), and protein (11%), respectively.	(Gopalakrishnan et al., 2016)
Rice	Zn	*Sphingomonas sp. SaMR12*, and *Enterobacter sp. SaCS20*	Enhancement in DTPA-Zn concentrations in rice rhizosphere	(Wang et al., 2014)
Wheat	Zn and Fe	*Exiguobacterium aurantiacum*	Inoculation with MS-ZT10, shows sixfold increase in Zn and Fe concentration	(Shaikh & Saraf, 2017)
Rice	Zn	*Bacillus sp*. and *Bacillus cereus*	Increased Zn translocation toward grains and increased production of 22%–49% and 18%–47%, respectively, for basmati-385 and super basmati rice varieties	(Shakeel et al., 2015)
Wheat	Zn	*Arthrobacter sp. DS-179*	Twofold increase in grain Zn content	(Singh et al., 2017)
Rice	Zn	*Acinetobacter*	Increased total Zn uptake per pot by 52.5% and the concentration of methionine by 38.8% in grain	(Vaid et al., 2014)
Chickpea	Fe and Zn	*Funneliformis mosseae; Rhizophagus irregularis*	5% and 16% increase in Fe and Zn concentrations, respectively.	(Pellegrino & Bedini, 2014)
Soybean	Se	*Paraburkholderia megapolitana MGT9*	Increased 7.4 folds higher Se content in leaves	(Trivedi et al., 2020)

thus improving nutrient bioavailability. Nanostructures with Zn-fortified cores surrounded by Mn carbonate shells improve Zn use efficiency in rice by delivering micronutrients to plant's roots. Mn nano-encapsulation with Zn has been shown to enhance grain yield and reduce nutrient loss (Yuvaraj & Subramanian, 2020). ZnO nanoparticles, with an average size of 25 nm, improve maize yield and increase the Zn content primarily in the grain (P. Sharma et al., 2022). Nano-materials can boost micronutrient efficiency due to their high water solubility, capacity to permeate plants quickly, large surface area, non-toxicity, and potential to mitigate environmental pollution (Kalra et al., 2020). Applying Fe, Mn, Cu, and Zn as liquid fertilizers via foliar sprays can expedite nutrient uptake compared to soil application. When this method is employed for nano-fertilizers, the stomata (when open) and leaf epidermal cells actively participate in nutrient absorption (Predoi et al., 2020). Nano-fertilizers promote plant development by stimulating meristematic activity. Nitrogen-based nano-fertilizers enhance the dry weight of mint plant (Mahil & Kumar, 2019), while Fe nano-fertilization increases carbohydrate and protein synthesis in maize (Iqbal & Umar, 2019). Using nano-fertilizers presents a sustainable, cost-effective approach to improve soil fertility, crop yield, and quality. In pumpkin, SiO2 nanoparticles improve water-use efficiency, photosynthetic pigments level, and carbonic anhydrase activities (Javed et al., 2022). Additionally, TiO_2 has been found to modulate photoreduction activity and inhibit linolenic acid in chloroplasts' ETC, aiding oxygen evolution (Siddiqi & Husen, 2017).

Nano-biofortification of crops, like wheat, has gained attention as a viable approach for improving the nutrient content (K. Khan et al., 2021). The Zn content in durum wheat grains has been enhanced using Zn-complexed chitosan nanoparticles (Dapkekar et al., 2018; Doolette et al., 2020) and foliar application of ZnO nano-fertilizer resulted in improved Zn accumulation in various plant parts (Hussain et al., 2021). Increased Mn accumulation has been reported with nano-Mn fertilizer application in mung beans (Pradhan et al., 2013) and wheat (Dimkpa et al., 2018). Nano-encapsulation offers an effective approach for developing nutrient-fortified crops, addressing malnutrition by improving nutrient bioavailability. While nano-fertilizers hold significant promise for enhancing nutrient use efficiency and yields in changing climates, it is essential to recognize and tackle their limitations and potential risks for responsible and sustainable implementation. Nano-fertilizers may negatively impact soil health and disrupt ecosystem balance, potentially leading to long-term environmental consequences. To mitigate this, comprehensive studies are required to understand the environmental fate of nanoparticles. Nano-fertilizers, which can incorporate soil-sustaining elements such as biochar, humic acids, and plant-derived extracts, hold significant potential when combined with organic matter like compost and cover crops to enhance soil health and nutrient availability. To overcome this, stringent design criteria should be established, using safe biodegradable materials. Regular toxicity assessments must be conducted following standardized testing protocols. Moreover, nano-fertilizers may be cost-prohibitive, limiting accessibility to a broader range of farmers, particularly in developing regions. It is important to investigate cost-effective synthesis methods and scalable production processes to overcome this. Regulatory uncertainties also pose a barrier to the widespread adoption of nano-fertilizers. To overcome this, clear regulatory frameworks with standardized testing procedures must be developed, and international collaboration is essential. Engaging with regulatory bodies to establish safety, efficacy, and responsible use guidelines will ensure proper oversight. Additionally, concerns about the accumulation of nanoparticles in plant tissues and potential health impacts raise food safety questions. Strategies to minimize nanoparticle accumulation in crops, such as controlled-release formulations or surface modifications, should be explored. Developing crops with reduced nanoparticle uptake through breeding or genetic engineering could also be beneficial. Finally, public perception and ethical concerns regarding the use of nanotechnology in agriculture may impact its social acceptance. To address this, transparency and dissemination of accurate information to farmers by organizing public awareness campaigns are important. A comprehensive approach that emphasizes the potential benefits of nano-fertilizers, while addressing their limitations and risks, along with practical strategies for mitigation, will contribute to the responsible and impactful integration of nano-fertilizers in agriculture.

4 | CONVENTIONAL BREEDING METHODS FOR ACHIEVING BIOFORTIFICATION

Although biofortification through mineral fertilizers or foliar sprays may increase the nutritional density of phloem-fed tissues, including seeds and fruits (Saltzman et al., 2017), its effectiveness is often limited by the restricted movement of nutrients in the phloem. For instance, Zn's low mobility restricts its deposition in edible plant parts. Alongside modern biotechnological approaches and advanced phenotyping tools, conventional breeding techniques have proven to be powerful tools for enhancing the micronutrient content of improved varieties in major crops. Plant breeding may help in increasing the nutritional content of staple crops without sacrificing yield or farmer-preferred agronomic traits. The development of micronutrient-efficient crop cultivars lowers the demand for fertilizer inputs and simultaneously improves crop nutritional quality in low-fertility soils by increasing both yield and micronutrient concentration. This strategy involves crossing between agronomically superior and economically beneficial cultivars that are high in micronutrient content (Alloway, 2009; Naveed et al., 2020; Shekari et al., 2015). The crop breeding approach includes screening germplasm for genetic variability, selecting micronutrient-rich resources, pre-breeding parental cultivars, and designing molecular markers to reduce costs and accelerate the breeding process. This approach relies on the genetic diversity present in crops, allowing plant breeders to exploit diverse genetic resources from primary, secondary, and tertiary gene pools to identify the key genes required for developing biofortified cultivars (Jha & Warkentin, 2020). To access the influence of environmental factor or genotype × environment interaction on micronutrient enhancement, promising lines are evaluated across a wide range of target environments. Several biofortified varieties of various crops with substantial gains in essential micronutrients have been developed using conventional breeding approaches (Saltzman et al., 2017; Sheoran et al., 2022). New biofortified varieties such as iron-rich beans and pearl millet, vitamin A rich orange sweet potatoes, orange maize and yellow cassava, and zinc-rich maize, rice, and wheat have been developed. These biofortified crops are developed to fill dietary intake gaps for Zn, Fe, and vitamin A based on consumption patterns. The released varieties have been formally approved by relevant authorities in their respective countries, highlighting the importance of breeding interventions in improving micronutrient level in crops and contributing to nutritional security. In Africa, orange-fleshed sweet potato (OFSP) has been biofortified with carotene concentrations ranging from 30 to 100 mg L^{-1}, compared to indigenous varieties, which contain less than 2 mg L^{-1} (Cong et al., 2009; Unnevehr et al., 2007). Biofortified white maize exhibited greater yield and improved agronomic traits, such as drought tolerance and disease resistance (Wang et al., 2014). A genetic diversity analysis was conducted in sorghum to identify lines with high Zn and Fe concentrations in seed. These lines were grouped based on their specific combining ability (SCA), providing insights into the genetic potential for enhancing micronutrient content in sorghum. Higher SCA than general combining ability for grain Zn and Fe contents indicated the contribution of the non-additive gene to the improvement of the nutritional trait. The presence of heterosis in agronomic traits and grain Fe content in hybrids suggests that intrapopulation improvement for micronutrients is likely advantageous. Various investigations have been undertaken to determine genetic diversity for micronutrient assessment (Dutta et al., 2020). Genetic variation among cultivars influences their response to nutrient availability, leading to differences in uptake and utilization efficiencies. A thorough understanding of genetic diversity enables the screening of more effective genotypes with improved root absorption, translocation, and utilization efficiency. Screening for Fe-efficient genotypes has addressed Fe deficiencies in several crops. Similarly, Zn-efficient genotypes have also been preferred for their tolerance to Zn depletion. The mutant breeding approach, which employs irradiation and chemical treatments to induce genetic variation, can also be utilized to improve grain quality, although no beneficial results have yet been obtained. However, traditional breeding is time-consuming and relies entirely on genes or alleles already present in the gene pool of crops, which limits its effectiveness. To overcome these constraints, researchers utilize modern molecular breeding techniques and genetic engineering tools to accelerate the process.

5 | MOLECULAR BREEDING APPROACHES FOR ACHIEVING BIOFORTIFICATION

The understanding of the genetic underpinning of micronutrient content in grains has achieved limited success, primarily due to the complex nature of quantitative inheritance of this trait, along with the significant effect of genotype × environment interactions on elemental concentration. The limited knowledge of the genetic underlying nutrient composition, especially with minor elements in plants, is due to low to moderate heritability estimates (Manickavelu et al., 2017). Identifying genomic regions or quantitative trait loci (QTL) that account for substantial phenotypic variation is important for understanding the genetic basis of traits influenced by multiple genes, such as grain micronutrient content (Boncompagni et al., 2018; Oliva et al., 2020). With the advancement of genomics resources, molecular marker technologies have increasingly been used to map genes associated with biofortification traits and introgression into elite cultivars. Molecular breeding has been widely used to develop biofortified varieties of major crops, including cereals, pulses, millets, fruits, and vegetables (Jaiswal et al., 2019). However, grain micronutrient content is controlled by polygenes, making trait dissection a complex challenge. Comprehensive investigations have been conducted and are ongoing for improving grain quality traits in cereals and legume crops, including rice, wheat, maize, and sorghum, resulting in significant phenotypic variation discovered for quality traits, amino acid composition, micronutrient density, and protein content (Table 2).

Many studies in rice on QTL mapping for Zn and Fe content have been conducted using different mapping populations (Sharma et al., 2023). In total, around 80 QTLs associated with Zn and Fe concentrations have been reported in rice. A major effect QTL for Zn content has been identified in the wild species and deepwater rice variety, which accounts for ≥30% phenotypic variation (Neelamraju et al., 2012). Similarly, Anuradha et al. (2012), detected 14 QTLs on chromosomes 7 and 12 linked with Zn and Fe content in rice grain. Likewise, recently Swamy, Descalsota et al. (2018) and Swamy, Kaladhar, et al. (2018) reported candidate genes associated with Zn content, such as *OsNRAMP*, *OsNAS*, *OsZIP*, *OsYSL*, *OsFER*, and *OsZIFL* in rice. This will aid in marker-assisted breeding and contribute to a better understanding of the genetic basis for grain micronutrient content. In addition, QTLs for Mn concentration have been identified on rice chromosomes 3, 7, and 8 (C. Liu et al., 2017). Notably, QTL on chromosome 3 exhibits synteny with corresponding regions in maize and sorghum (Minx et al., 2005). Another major QTL (*qGMN7.1*) on chromosome 7, explaining 23% phenotypic variance (PVE) for Mn content, was detected (C. Liu et al., 2017). Additionally, five potential genes (*LOC_Os07g15350*, *LOC_Os07g15360*, *LOC_Os07g15390*, *LOC_Os07g15400*, and *LOC_Os07g15370*) have been identified within the 49.3 kb target region with fine mapping of this genomic region in rice. Subsequently, *LOC_Os07g15370* (*OsNRAMP5*) was identified as a candidate gene associated with increased grain Mn accumulation in rice. Recent developments in genomics and the ease of access to rice genome annotation facilitate the identification of genes and co-localized genomic regions, consequently facilitating the development of functional markers for marker-assisted selection (MAS) in biofortification breeding programs (Sharma et al., 2020).

Furthermore, genetic variability in wheat for grain micronutrient content allows the improvement of biofortification (Velu et al., 2014). CIMMYT is investigating genetic variation via its HarvestPlus initiative, that demonstrated the existence of favorable variation for grain quality traits among crop wild relatives in wheat (Velu, Tutus, et al., 2016; Velu, Crossa, et al., 2016). A major locus (*Gpc-B1*) for micronutrient concentrations was detected on chromosome 6 using recombinant chromosome substitution lines in wheat (Distelfeld et al., 2007). Crespo-Herrera et al. (2016) identified a major locus, *QGZn.cimmyt-7B_1P2*, on chromosome 7B associated with grain Zn content in wheat, accounting for 32.7% PVE. Similarly, five genomic regions for Zn content, explaining 32% PVE, and four genomic regions associated with grain Fe content, accounting for 20% PVE, were reported in wheat (Krishnappa et al., 2017). Additionally, in wheat recombinant inbred line (RIL), a locus (*QGFe.cimmyt-*

TABLE 2 Molecular breeding studies for enhancement of micronutrient's in major cereals and legumes.

Crops	Sequencing approach/Platform	Mapping Population/Germplasm	Target traits	Significant outcomes	References
Rice	SSR markers	Teqing × *O. rufipogon* (IL)	Micro-element and macro-elements	Identified three QTLs (*qZn5-1*, *qZn8-1*, and *qZn12-1*) for zinc content on chromosome 5 with 5% PVE, chromosome 8 with 19% PVE and chromosome 12 with 9% PVE	(Garcia-Oliveira et al., 2009)
	SSR markers	Madhukar × Swarna (RILs)	Fe and Zn content	Identified 13 genomic regions for Fe and Zn content possessing 29%–71% PVE.	(Kumari et al., 2012)
	SSR markers	Sasanishiki × Habataki (BIL)	Zn content	Detected two major QTLs (*qSZn2* and *qSZn12*) for Zn content on chromosome 2 and 12 with 16.7%–21.3% PVE	(S. Ishikawa et al., 2010)
	SSR markers	Goami 2 × Hwaseonchal (DH)	Fe and Zn content	Identified seven QTLs for Fe content with 11.6%–40.50% PVE and 14 QTLs for Zn content showed 12.6%–46.8% PVE	(Jeong et al., 2020)
	7 K SNP array	IR05F102 × IR69428 (DH)	Fe and Zn concentrations	Two major QTLs (*qFe9.1* and *qFe12.1*) were identified for Fe on chromosome 9 and 12 with 11.79%–13.34% PVE, and three major QTLs (*qZn5.1*, *qZn9.1*, and *qZn12.1*) for Zn with 12.15%–15.26% PVE.	(Calayugan et al., 2020)
	6 K-SNP chip	IR64 × IR69428 and BR29 × IR75862 (DH)	Grain mineral elements	Detected 50 QTLs for grain element concentration with 8.6%–36.8% PVE	(Descalsota-Empleo et al., 2019)
	6 K-SNP chip	PSBRc82 ×Joryeongbyeo and PSBRc82 × IR69428 (DH)	Biofortification traits	Identified 59 QTLs for 13 biofortification traits with 6.8%–43% PVE	(Swamy et al., 2018a)
	SSR markers	Two BC_2F_2 populations	Fe and Zn concentrations	Sixteen metal homeostasis genes detected to co-locate with ten genomic regions linked with Fe and Zn concentrations	(Swamy et al., 2018b)
	InDel markers	Lingshui population (RIL)	Cd, Zn and Se concentration	Identified one major QTL (*GZC6*) on chromosome 6 explaining 16.4% PVE for Zn concentration and one major QTL (*GSC5*) for Se concentration on chromosome 5 with 13.8% PVE	(C. Liu et al., 2020)
	Genotyping-by-sequencing	MAGIC (16 founders of indica and japonica pools)	Quality traits	Identified 22 candidate genes on chromosome 7 and 10 candidate genes on chromosome 5 associated with Zn content	(Zaw et al., 2019)
	SSR markers	*O. sativa* 'Nipponbare' and *O. meridionalis* W1627 (BIL)	Grain Zn concentration	Identified *qGZn9b* QTL which provides a favourable allele associated with high Zn concentration	(R. Ishikawa et al., 2017)
	InDel markers	93-11 × PA64s (RIL)	Mn concentration	Fine mapping of *qGMN7.1* genomic region to a 49.3 kb, harbouring *OsNRAMP5* gene associated with uptake of Mn and Cd	(C. Liu et al., 2017)

(Continues)

TABLE 2 (Continued)

Crops	Sequencing approach/Platform	Mapping Population/Germplasm	Target traits	Significant outcomes	References
	SSR markers and Genotyping-by-sequencing	PR116 × Ranbir Basmati	Zn content	Identified one major QTL (*qZPR.1.1*) on chromosome 1 with 37.84% PVE and 15.47% PVE for another major QTL (*qZPR.11.1*) on chromosome 11 for Zn content	(Suman et al., 2021)
	SNP markers	Aus Panel	Fe content	One candidate gene-*nicotianamine synthase OsNAS3* has detected, which is associated with Fe content in grain	(Talukdar et al., 2022)
	SSR markers	MTU 1010 × BR 2655	Zn content	Detected one stable QTL (*qZn-2.1*) on chromosome 2 with 7.74% PVE (wet season) and 10.2% PVE (dry season)	(Rathod et al., 2021)
Wheat	Diversity Arrays Technology	Saricanak98 × MM5/4 and Adana99 × 70,711 (RIL)	Fe and Zn concentrations	Identified stable genomic region on chromosomes 1B (*QGzn.ada-1B* and *QGzn.sar_1B*) and 6B (*QGzn.ada-6B* and *QGzn.sar_6B*), and two overlapped QTLs on chromosome 2B for Zn and Fe concentration	(Velu et al., 2017)
	SSR markers and Diversity Arrays Technology	cv. Berkut × cv. Krichauff (DH)	Zn, Fe and protein concentration	Identified, two major QTLs for Zn content on chromosome 1B and 2B with 23.1%–35.9% PVE, one QTL for Fe concentration on chromosome 2B with 22.2% PVE and one QTL for grain protein on chromosome 1A, explaining 17.7% PVE, respectively.	(Tiwari et al., 2016)
	Genotyping-by-sequencing	Seri M82 × SHW CWI76364	Fe and Zn concentrations	Identified major QTL for GZn and GFe on chromosome 4BS, explaining 19.6% PVE and also reveals pleiotropic effect for traits	(Crespo-Herrera et al., 2016)
	SSR markers	WH542 × Synthetic derivative	Zn, Fe and protein concentration	Detected four QTLs for Fe with 20.0% PVE, five QTLs for Zn with 32.0% PVE and two QTLs for PC, explaining 24.1% PVE.	(Krishnappa et al., 2017)
	SSR markers and Diversity Arrays Technology	SHW-L1/Chuanmai 32; SC and Chuanmai 42/Chuannong 16; CC (RIL)	Micronutrient concentrations	Identified 26 QTLs for the five traits (Se, Fe, Zn, Cu, and Mn) in the SC population, explanging 4.8%–28.5% PVE and 13 QTLs for four traits (Se, Fe, Zn, and Mn) in the CC population, attributing 6.9%–35.1% PVE	(Pu et al., 2014)
	Diversity Arrays Technology	*T. spelta* H+ 26 (PI348449) × *T. aestivum* cv. HUW 234 (RIL)	Zn and Fe concentration	Detected three major QTLs in which one QTL for Zn (*QZn.bhu-2B*) with 16.46% PVE and two QTLs (*QFe.bhu-1A.3* and *QFe.bhu-3B*) for Fe accumulation with 16.55% and 25.95% PVE	(Srinivasa et al., 2014)
	Diversity Arrays Technology	Roelfs F2007 × Chinese parental line (RIL)	Micronutrients concentration	Identified one major QTL (*QGZn.co-5A*) on chromosome 5A with 14.22% PVE for Zn content and one major QTL (*QGFe.co-3B.1*) on chromosome 3B for Fe content explaining 14.56% phenotypic variance	(J. Liu et al., 2019)
	Diversity Arrays Technology	Zinc-Shakti × Kachu (RIL)	Fe concentration	Detected two major QTLs (*QFeC-2A.2* and *QFeC-6B.1*), accounting for 10.1% and 10.2% PVE	(Rathan et al., 2021)

(Continues)

TABLE 2 (Continued)

Crops	Sequencing approach/Platform	Mapping Population/Germplasm	Target traits	Significant outcomes	References
	Illumina iSelect 90 K Infinitum SNP array	HPAM panel (330 wheat lines)	Zn concentration	Identified one major genomic region on chromosomes 7B, explaining 10.4% PVE and harbouring *zinc finger motif* and *metal-ion binding genes*	(Velu et al., 2018)
	Diversity Array Technology	Synthetic hexaploid wheat × *T. spelta* L. derived line	Zn and Fe concentrations	Detected one major QTL (*QGZn.cimmyt-7B_1P2*) for Zn concentration on chromosome 7B with 32.7% PVE and one major QTL (*QGFe.cimmyt-4A_P2*) for Fe concentration on chromosome 4A, accounting 21.14% PVE	(Crespo-Herrera et al., 2017)
Maize	SNP markers	Ye478 × Wu312 (RIL)	Mineral concentration	Identified cluster at Bin 4.05/4.06 with stable QTLs (*qMnCC4-1* and *qMnCC4-2*) for Mn concentration, explaining 12.88%–15.33% phenotypic variance	(Gu et al., 2015)
	SSR and SNP markers	By804 × B73 (RIL)	Carotenoids related traits	Detected nine major QTLs (*qbc6-1*, *qbc/bcry10-1*, *qbc/tc10-1*, *qbcry6-1*, *qlut6-1*, *qtc6-1*, *qtva6-1*, *qzea10-1*, and *qzea/tc10-1*) for carotenoids related traits with 16.91%–43.71% PVE	(Jittham et al., 2017)
	SSR and SNP markers	B84 and Os6-2	Biofortification traits	Identified three QTLs (Fe/P, Zn/P, and Mg/P) which are co-localized on chromosome 3, in close proximity to *phytase* genes (*ZM phys1* and *phys2*)	(Šimić et al., 2012)
	SSR markers	178 × P53 (RIL)	Mineral concentration	Detected five QTLs (*qZn7-3*, *qZn7-4*, *qMn7-5*, *qMn7-6*, and *qMn7-7*) flanked by same marker intervals (phi057-bnlg1380) in single environment analysis and two genomic regions (*qmZn7-3* and *qmMn7-2*) are identified in multi-environmental trials analysis for Zn and Mn concentration	(H. Zhang et al., 2017)
	SSR markers	W64a × A632 (F_2:F_4) and testcross progeny with AE335.	α and γ tocopherol	Identified one major QTL for α -tocopherol with 19.6% PVE and one major QTL for γ-tocopherol, accounting 23.6% PVE on chromosome 5	(Wong et al., 2004)
	Genotyping-by-sequencing	N6 × NC296 and E2558W × Co125	Vitamin E content	Identified candidate gene *homogentisate phytyltransferase* (*ZmVTE2*) which is linked with tocochromanol pathway	(Fenton et al., 2018)
Chickpea	Genotyping-by-sequencing	MNK-1 × Annigeri 1	Fe and Zn concentrations	Identified five major QTLs (*CaqFe4.2*, *CaqFe4.3*, *CaqFe4.4*, *CaqFe4.5*, and *CaqFe5.2*) for Fe concentrations, explaining 10.5-13.4% phenotypic variance; and six major QTLs (*CaqZn4.1*, *CaqZn4.3*, *CaqZn4.4*, *CaqZn4.5*, *CaqZn4.6*, and *CaqZn5.1*) for Zn concentrations with 10.2%–13.7% PVE.	(Sab et al., 2020)

(Continues)

TABLE 2 (Continued)

Crops	Sequencing approach/Platform	Mapping Population/Germplasm	Target traits	Significant outcomes	References
	50K Axiom *Cicer*SNP array	CDC Jade × CDC Frontier, CDC Cory × CDC Jade and ICC4475 × CDC Jade	Carotenoid	Detected three major QTLs for *β*–carotene concentrations (*q-Crt-8-CJ*, *q-Crt-8-JF*, and *q-Crt-8-IJ*) on chromosome 8, explaining 58%–69% phenotypic variance and also reported SGR gene	(Rezaei et al., 2019)
	Illumina GoldenGate SNP genotyping assay	ICC 4958 × ICC 8261	Fe and Zn content	Identified three major QTLs (*CaqFe1.1*, *CaqFe3.1*, and *CaqFe4.1*) on chromosome 1, 3 and 4 for Fe content with 21.1%–23.4% PVE; and two major QTLs (*CaqZn2.1* and *CaqZn3.1*) for Zn content chromosomes 2 and 3, explaining 18.7%–21.8% PVE	(Upadhyaya et al., 2016)
	Whole-genome sequencing data	258 diverse set	Nutritional traits	Detected 62 significant MTAs possesing up to 28.63% PVE of which nine are localized within genes regulating *GPCR pathway*, *intracellular signal transduction*, and *oxidation–reduction process*	(Roorkiwal et al., 2022)
	SNP markers	94 diverse *C. arietinum* accessions	Zn and Fe content	Identified eight significant MTAs on chromosome 1, 4, and 4 for Zn and Fe content	(Diapari et al., 2014)
Common bean	SSR markers	DOR364 × G19833	Zn and Fe content	Identified eleven QTLs (five QTLs for Fe and six QTLs for Zn) are clustered on L.G. B11, explaining up to 47.9% phenotypic variance	(Blair et al., 2009)
	SSR and RAPD markers	G21242 × G21078	Zn and Fe content	Identified six QTLs (*Fe-ICP2a*, *Fe-ICP7a*, *Fe-ICP9a*, *Fe-AAS2a*, *Fe-AAS6b*, and *Fe-AAS6c*) for Fe content with 33.5%–47.4% PVE and three QTLs (*Zn-AAS2c*, *Zn-AAS7c*, and *Zn-AAS8c*) for Zn content, accounting 13.5%–18.6% PVE	(Blair et al., 2011)
	AFLP, SSR and SCAR markers	Xana× Cornell 49242	Seed chemical content	Detected eight QTLs in three important genomic regions (*P gene* on chromosome Pv07, *Fin gene* (Pv01), and *Phaseolin*, a locus (Pv07)	(Casanas et al., 2013)
	ddRAD-seq	192 genotypes diverse panel	Zn content	One candidate gene *Phvul001G233500* is identified which encodes an *E3 ubiquitin-protein ligase*	(Caproni et al., 2020)
Lentil	Diversity Array Technology	ILL 8006 × CDC Milestone	Fe concentration	Identified 21 QTLs across six linkage groups (LGs) for Fe concentration, accounting 5.9%–14.0% phenotypic variance	(Aldemir et al., 2017)
	SSR and SNP markers	PI 320937 × Eston (RIL)	Se uptake in seed	Detected four QTL regions on L.G.2 and L.G.5 for seed Se concentration, with 6.3%–16.9% PVE	(Ates et al., 2016)
	SSR markers	96 diverse germplasm lines	Zn and Fe content	Identified three MTAs for Fe content with 9%–11% PVE and four MTAs for Zn content explaining 14%–21% PVE	(Singh et al., 2017)
	SNP markers	138 cultivated accessions	Zn and Fe content	Identified two significant MTAs, one for Fe and one for Zn concentration, explaining 9%–21% phenotypic variance	(Khazaei et al., 2017)

(Continues)

TABLE 2 (Continued)

Crops	Sequencing approach/Platform	Mapping Population/Germplasm	Target traits	Significant outcomes	References
	Diversity Array Technology	CDC Redberry × ILL7502	Mn concentrations	Identified six major QTLs (*MnQTL1.1*, *MnQTL1.2*, *MnQTL3.1*, *MnQTL3.2*, *MnQTL3.3*, and *MnQTL7.1*) on three L.G. 1, 3, and 7 for Mn concentration, accounting 15.3%–24.1% PVE	(Ates et al., 2018)
Soybean	GoldenGate assay for a Universal Soy Linkage Panel	Williams 82 × DSR-173, Williams 82 × NKS19-90 and Williams 82 × Vinton 81	Mineral, cysteine, and methionine concentrations	Identified novel major QTL for Cys (and Cys + Met) on L.G. 2 in DSR population with 17% PVE and another QTL for Cys (and Cys + Met) on L.G. 20, explaining 16% phenotypic variance	(Kastoori Ramamurthy et al., 2014)
	SSR markers	SS-516 × Camp	Calcium content	Detected four QTLs (*Ca1*, *Ca2*, *Ca3*, and *Ca4*) on L.Gs. A2, I, and M for calcium content, explaining 9.7%–16.3% of phenotypic variance	(B. Zhang et al., 2009)
	SSR markers	AC Hime × Westag-97 and Leo × Westag-97	Cd accumulation	Identified major QTL (*Cda1*) for Cd concentration on L.G. K with 57.3% PVE	(Jegadeesan et al., 2010)
	SSR markers	OAC Bayfield × Hefeng 25	Vitamin E contents	Identified six major QTLs (*QαC2_1*, *QγA2_1*, *QγC2_1*, *QγO-1*, *QδI_1*, and *QTVE D1b_1*) for four traits (α-Toc, γ-Toc, δ-Toc, and Total VE), explaining 10.2%–16.7% phenotypic variance	(H. Li et al., 2010)
	SNP markers	TK780 × B04009	Tocopherol content	Detected seven major QTLs (*qαTC-9*, *qαTC-12*, *qαTC-9*, *qαTC-12*, *qδTC-19*, *qγTC-7*, and *qTTC-1*) for tocopherol content, explaining 12.7%–39.4% phenotypic variance	(Park et al., 2019)

Abbreviations: PVE, phenotypic variance; QTL, quantitative trait loci.

4A_P2) for grain Fe content was detected on chromosome 4A, accounting for 20% PVE (Crespo-Herrera et al., 2017).

Various mapping studies have been carried out to identify the genomic regions responsible for biofortification traits in maize. In maize (Jittham et al., 2017), using RIL population (By 804 × B73) identified 24 major QTLs for kernel carotenoid traits, accounting for 16.91%–43.71% PVE. Another study reported two major genomic regions (*qZn6-3* and *qZn6-5*) for Zn content, explaining 11.7%–16.8% PVE and seven major genomic regions (*qMn1-1*, *qMn1-2*, *qMn1-5*, *qMn3-2*, *qMn3-3*, *qMn3-4*, and *qMn4-3*) for Mn content with 10.49%–15.35% PVE (H. Zhang et al., 2017). Grain legumes, like cereal crops, keep on contributing significantly in providing proper nutrition owing to their high protein and mineral content. Various legume cereals, including sorghum and pearl millet, were initially believed to have little genetic and genomic resources. Recent developments in genomic tools in recent decades have facilitated the development of genetic stocks. In recent years, in pearl millet, various mapping populations developed for Zn and Fe content from a diverse genetic background panel of Asian, American, and African origins (S. Kumar et al., 2016). A major QTL for Fe and Zn content was detected in RIL (ICMB 841-P3 × 863-P2) on chromosome 3, explaining 19% PVE for Fe and 36% PVE for Zn (S. Kumar et al., 2016). Similarly, two loci associated with Fe and Zn content have been identified on chromosomes 3, 5, and 7, exhibiting 16% and 42% PVE (S. Kumar et al., 2016). In sorghum, important findings related to the genetic regulation of grain composition via mutation reported QTL for amylose content located 12 kb from the *waxy* locus (Lichtenwalner et al., 1978; Rooney & Pflugfelder, 1986). Similarly, a major QTL for crude fat was detected on chromosome SBI-10, accounting for 28.1% PVE (Boyles, 2016).

Although QTL mapping proved important in detecting genomic regions linked to traits of interest, its resolution is often restricted by the use of biparental populations. The power of genome-wide association studies (GWAS) to dissect traits of interest in diverse sets of germplasm makes this method effective for linking biofortified traits' variation to genetic variants. In rice, association mapping using 378 accessions identified 20 marker trait associations (MTAs) linked with Fe, Zn, Se, Cd, and lead (Pb) mineral elements (Y. Huang et al., 2015). Significant MTAs detected on 5, 7, and 11 chromosomes indicate substantial possibilities for rice breeding (Y. Huang et al., 2015). Another study (Nawaz et al., 2015) using USDA mini core collection detected 37 MTAs linked to the mineral content of Zn, Fe, Mn, Mg, and K. In wheat, GWAS using a diverse panel of 353 European wheat varieties detected associations for grain Ca accumulation (Alomari et al., 2017). In maize, association analysis using 923 lines for kernel Fe and Zn content identified 20 single nuceleotide polymorphisms (SNPs) associated with Zn content and 26 MTAs for Fe content. The findings assist in maize biofortification and could help in dissection of genomic regions associated with target traits (Hindu et al., 2018). GWAS studies in sorghum identified significant MTAs associated with mineral elements, polyphenol, protein, fat, and starch content (Rhodes et al., 2017; Shakoor et al., 2016). Another association study in sorghum using 195 accessions detected significant MTA for genes linked with the starch synthesis pathway (De Alen et al., 2010).

Nowadays, genomic selection (GS) is thought of as more efficient for complex quantitative traits that are regulated by small effect/minor QTLs. GS enables the early prediction of target biofortification traits in breeding, prior to extensive multi-location trials or long-term assessment cycles. It additionally facilitates the prediction of individual performance without phenotypic evaluation, thereby enabling genetic gain for improving biofortification traits (Battenfield et al., 2016). In wheat using GS approach, models have been trained utilizing 5520 lines with 3075 SNPs. The investigation showed that the GS model's prediction precision increased with time, from 0.32 for grain hardness to 0.62 for mixing time (Battenfield et al., 2016). In maize, GS investigation (Owens et al., 2014) reported a prediction precision of up to 0.71 and an average of 0.43 for grain carotenoid traits. Deploying GS with speed breeding can enable breeding to be more effective in improving the biofortification traits' concentration based on breeding values.

6 | TRANSGENIC APPROACHES

Transgenic techniques offer a feasible alternative way for developing biofortified crops, particularly when there is limited or no genetic variability available for nutritional traits in plant species, such as in case of golden rice (Mrunalini et al., 2020). These approaches aim to modify plant gene sequences to enhance micronutrient deposition in plant edible parts and improve their bioavailability for human consumption (Kaur et al., 2020). Transgenic approach enables the introduction of desirable traits by transferring new genes, overexpressing existing genes, or silencing unfavorable genes. Developing transgenic crops requires understanding gene function, followed by deployment of these genes to alter plant metabolic pathways (Christou & Twyman, 2004). The expression of transgene facilitates micronutrient re-translocation across tissues, increasing their bioavailability and efficacy and contributing to the remodeling of biochemical pathways.

Genetic engineering has emerged as a sustainable and cost-effective alternative to conventional fortification methods for increasing plant micronutrients level (Van Der Straeten et al., 2020). Using transgenic techniques, many crop species have been biofortified with micronutrients. In polished rice, simultaneous increases in Fe, Zn, and β-carotene levels were achieved (Singh et al., 2017). Other successful transgenic crops include high-lysine maize, soybeans with unsaturated fatty acids, provitamin A- and iron-rich cassava, and provitamin A-rich golden rice. Additionally, transgenic rice overexpressing *Fe regulator-carrier-like protein 1* showed increased Fe and Zn accumulation (Lee & An, 2009). Phytic acid, the primary storage form of phosphorus in seeds, acts as an anti-nutritional factor that chelates minerals and restricts the absorption of important micronutrients such as Zn, Fe, and Ca (R. K. Gupta et al., 2015). Transgenic approaches can be used to reduce the phytic acid content in food crops, thus alleviating malnutrition by improving the nutritional quality of crops deficient in nutrients due to anti-nutritional factors. According to Wirth et al. (2009), co-expression of Arabidopsis *synthase*, Aspergillus *phytase*, and bean *ferritin* and overexpression of ferritin protein in rice and soybean significantly increased the concentration of Fe and Zn in rice, compared to wild type. Another study revealed that overexpression of the Arabidopsis vacuole Fe transporter (*VIT1*) in transgenic cassava plants increased Fe content up to 70-fold compared to control (Narayanan et al., 2019). Moreover, enhancing the production of metal chelators such as mugineic acid (MA) and nicotianamine has been shown to improve Fe and Zn concentrations in edible plant parts (Slamet-Loedin et al., 2015). Although genetic biofortification offers a feasible solution for combating malnutrition, resistance to transgene technologies remains a major barrier. Many countries have strict regulations on this technology. In Table 3, key biofortified cereal and legume crops, along with their significant outcomes, are highlighted.

7 | GENOME EDITING TECHNOLOGY

Several genome editing approaches, including Clustered Regularly Interspaced Short Palindromic Repeats (CRISPR)-Cas and meganucleases, like Zn-finger nucleases (ZFNs) and transcription activator-like effector nucleases (TALENs), hold great potential for crop improvement (Ansari et al., 2020). Several plants, including Arabidopsis, wheat, rice, barley, and tobacco, have been genetically modified utilizing these meganucleases (Sedeek et al., 2019). However, ZFN and TALEN are less widely used compared to CRISPR-Cas due to higher cost, inefficiency, and time-consuming design process (Yin et al., 2017). In one study, CRISPR-Cas9 was used to knock out *OsZIP9*, a Zn-IRT-related protein involved in Zn absorption, to investigate its role in Zn accumulation. The edited rice plants, grown in low Zn hydroponic solutions, showed lower Zn concentration in roots and shoots compared to the wild type. This suggests that *OsZIP9* serves as a Zn flux transporter that promotes Zn uptake in rice (S. Huang et al., 2020). The CRISPR-Cas9 system was employed in rice to reduce the accumulation of toxic heavy metals such as Cd. Knocking out the rice metal transporter gene *OsNramp5* resulted in reduced Cd accumulation in the shoots and roots, which was advantageous for plant development (Tang et al., 2017). It is well established that Cd and Fe share common transporters in rice, including *OsNramp1*, *OsNramp5*, *OsIRT1*, and *OsIRT2* (Sasaki et al., 2012; Senoura et al., 2011). Knockout lines of *OsNramp5* exhibited higher expression of these Fe/Cd transporter genes, notably under Fe deficiency (Takahashi et al., 2014; Yang et al., 2014). The variation in Cd accumulations could be attributed to differential regulation of *OsNramp5* and the induction of different Fe/Cd transporter genes in the rice lines (Sasaki et al., 2012; Takahashi et al., 2014). Fortifying crops with β-carotene could help to overcome vitamin A deficiency in underdeveloped nations. Recently, the orange (or) gene, which triggers the accumulation of β-carotene in cauliflower, was edited using CRISPR-Cas9 to induce β-carotene accumulation in rice. In another study, high-carotenoid rice was developed by using the CRISPR-Cas9 by integrating a 5.2 kb carotenoid biosynthesis cassette (Dong et al., 2020). This cassette included coding sequences for two carotenoid biosynthesis genes, *SSU-crtI* and *ZmPsy30*, both driven by the endosperm-specific glutelin promoter isolated from Kitaake rice. *SSU-crtI* is a functional fusion of the chloroplast transit peptide from the pea ribulose-1,5-bisphosphate carboxylase-oxygenase (RUBISCO) small subunit and the *Erwinia uredovora* carotenoid desaturase, while *ZmPsy* encodes a maize phytoene synthase. The *nopaline synthase* (*nos*) terminator (from *Agrobacterium tumefaciens*) was used for transcription termination in both genes. Marker-free rice plants with increased carotenoid content and absence of detectable negative effects on plant morphology or yield were achieved, highlighting the potential of this technique for precise genetic improvement in crops. Whole-genome sequencing confirmed the absence of off-target mutations, further supporting the reliability and safety of this CRISPR-Cas9-mediated approach.

However, CRISPR-Cas9 has some shortcomings, including off-target gene cleavage, altered gene function, or genomic instability (Naeem et al., 2020). Additionally, CRISPR-Cas9-modified crops face regulatory restriction in several countries. For instance, CRISPR-modified crops have been exempted from genetically modified organism (GMO) regulations by the USDA; however, the European Union (EU) Court of Justice has imposed stringent GMO restrictions on it (Callaway, 2018). Aside from legal concerns, public acceptance of genome-edited crops remains a major issue. Given the potential of genome editing technologies, future research should focus on developing more nutritious, high-yielding food crops while also addressing regulatory and public acceptance challenges.

TABLE 3 Transgenic bio-fortified cereals and legumes crops with enhanced micronutrients.

Crops	Target traits	Significant outcomes	References
Rice	Fe and Zn content	Enhancement in endogenous nicotianamine levels in the shoots and seeds of transgenic rice with *HvNAS1* overexpression by *OsActin1 promoter/35S promoter*, leading to threefold greater rise in Fe concentration	(Masuda et al., 2009)
Rice	Fe content	Increase Fe-localization in seeds with overexpression of *OsYSL2* gene (*Fe-nicotianamine transporter*) via *sucrose transporter promoter*	(Ishimaru et al., 2010)
Rice	Zn content	*OsHMA1* expression is enhanced in Zn-deficient shoot tissues	(Lee et al., 2007)
Wheat	Fe content	Increased Fe accumulation in seed with overexpression of *TaVIT2* (*wheat vacuolar iron transporter*) via *endosperm-specific promoter*	(Connorton et al., 2017)
Wheat	Fe content	Endosperm-specific intragenic overexpression of the *TaFer1-A* gene enhanced 50%–85% grain iron concentration	(Borg et al., 2012)
Wheat	Fe and Zn content	Overexpression of the *Phytase* gene under the control of *D-hordein* and gluten in promoters enhanced Fe and Zn bioavailability in grains	(Abid et al., 2017)
Wheat	Zn content	Increase in Fe and Zn level in the grains with the overexpression of rice *OsNAS2* (*NICOTIANAMINE SYNTHASE 2*) gene	(Singh et al., 2017)
Maize	Fe content	Enhancement in Fe level via endosperm-specific co-expression of *ferritin* and *phytase* gene	(Drakakaki et al., 2005)
Wheat	Provitamin A content	Enhancement in grain carotenoid content via expression of *CrtB* and *CrtI* genes in transgenic wheat	(Wang et al., 2014)
Soybean	Sulfur amino acid	Improvement in sulfur amino acid content with the overexpression of *ATP sulfurylase* via *35S CaMV* promoter	(W. S. Kim et al., 2020)
Soybean	Oil and linoleic acid contents	Enhancement in oil and linoleic acid content with the overexpression of *GmDGAT2A* gene via *Gmole1* promoter	(Jing et al., 2021)
Barley	Phosphate bioavailability	Enhancement in phosphate bioavailability with the expression *HvPAPhy_a* gene	(Holme et al., 2012)

8 | COMPONENTS OF SIGNALING AND MICRONUTRIENT MOVEMENT IN CEREALS AND LEGUMES

Micronutrients are capable of being transported from various tissues to seeds, suggesting a pathway that passes through reproductive, root, stem, and leaf tissues (Figure 2). Plants absorb micronutrients from the soil in the form of mineral ions, which are subsequently transported via short- and long-distance transport systems according to the physiological and structural needs of plant organs. In rice, the acquisition of Fe involves both reduction and chelation mechanisms, whereas non-poaceae species employ reduction-based method. When a plant is starved of micronutrients, it activates specific signaling pathways and hormonal responses (Jung & McCouch, 2013). By activating the transporter genes, these connections can modify the root architecture to improve nutrient uptake and transport of mineral ions (Vigani et al., 2013). The uptake of micronutrients from the rhizosphere, the first stage in nutritional homeostasis, has been extensively investigated. Understanding the uptake-transport equilibrium is important to achieve higher micronutrient concentrations in biofortified seeds. A major challenge in micronutrient fortification is lack of knowledge about kinetic and metabolic processes governing micronutrient translocation to seeds. Recent studies have identified genes involved in the absorption and mobilization of Fe and Zn from various plant parts to the seeds (Sen Gupta et al., 2017; Urwat et al., 2021).

For a number of biological processes, including every enzyme in the ETC that occurs in mitochondria, Fe acts as a key component. Plants have developed various mechanisms for efficient absorption of Fe (S. A. Kim & Guerinot, 2007), such as secreting phyto-siderophore, which facilitate Fe acquisition. Fe is required for the activity of enzymes,

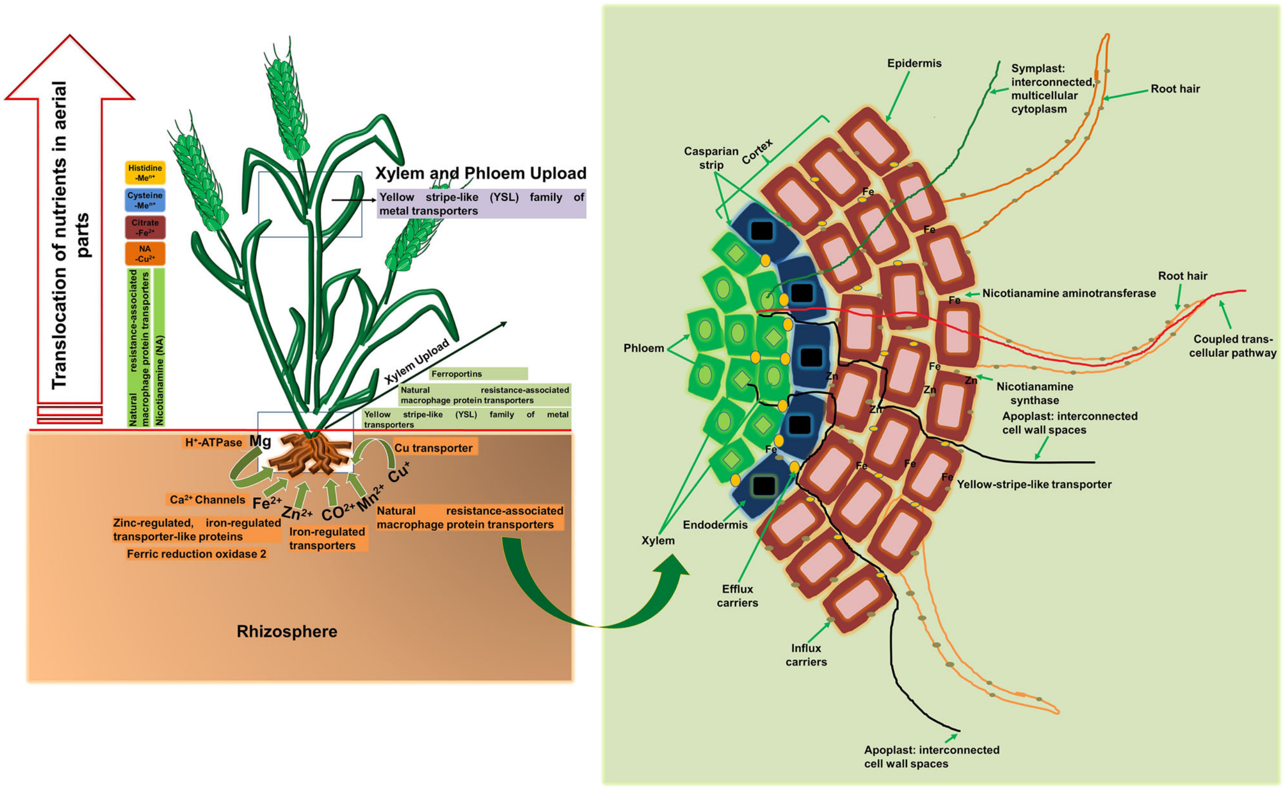

FIGURE 2 A schematic representation of the several transporters that transfer nutrients and minerals from the soil to the aerial parts, as well as the various pathways involved in mineral transport through the roots.

such as glycosyltransferases, decarboxylases, and dehydrogenases (Nunan & Scheller, 2003), and is important for mitochondrial superoxide dismutase activity, Photosystem II, and the biosynthesis of triglycerides and tetraterpenoids (Bowler et al., 1991). Fe is found in soil in two oxidation forms (Fe^{3+} and Fe^{2+}), with Fe^{3+} being the most common because it is highly soluble in an anaerobic environment with an acidic pH. Fe^{3+} can form insoluble hydroxides in alkaline soils, reducing its availability for plant uptake. Plants have evolved two main strategies (the reduction strategy and the chelation strategy) to actively absorb Fe from the soil when conditions are unfavorable. Dicotyledonous and non-grass plants generally employ the reduction strategy, which occurs at the root-rhizosphere transition in three steps. The Fe-absorption strategy II is used by graminaceous plants such as rice to absorb the Fe efficiently from Fe-deficient soils. This strategy is more effective than the reduction strategy and allows grasses to withstand severe Fe-deficient conditions. Plant root cells secrete phytosiderophores, such as MA, which chelate Fe^{3+} in the rhizosphere, facilitating Fe acquisition. For long-distance Fe transport, active root transporters load Fe from root cortical cells to the root stele. Fe^{3+}-DMA transporter genes, *OsYSL15* and *OsYSL18*, are expressed in developing grains (Lee & An, 2009). Overexpression of *OsNAS2* in rice resulted in a twofold increase in grain Fe concentration (Lee et al., 2012). Similarly, Ishimaru et al. (2010) observed a 4.4-fold increase in Fe in polished rice by overexpressing *OsYSL2* using phloem-specific *OsSUT1* promoter.

Mn plays an important role in metabolic function in plants due to its ability to rapidly transition oxidation states. In high pH soils, Mn deficiency is common, which affects yield, especially in monocots, where it increases susceptibility to pathogen infection and cold stress. Mn chelation via reductants, increase H^+ concentration, and Mn-binding ligands (Eaton et al., 2015). Potential candidates for Mn uptake include Zn- and Fe-regulated carrier protein families with nodes acting as important regulatory controllers in the allocations of Mn distribution to leaves, stem, and panicle in monocots (Yamaji & Ma, 2014). In rice, *OsNRAMP5* controls Mn uptake from soil and its transport in shoots (Yang et al., 2014). Micronutrient Zn is essential for both plant and human metabolism, being a part of several important enzymes (A. Singh et al., 2018). Zn deficiency negatively affects yield and human nutrition (Hotz & Brown, 2004). Zn deficiency in cereal is often due to low soil Zn availability, driven by factors such as soil pH and redox potential. Biofortification strategies, including Zn fertilization or genetic engineering, are promising approaches to address Zn deficiency in plants (White & Broadley, 2009). Zn is transported from the rhizosphere to roots, facilitated by mechanism such as oxidative stress tolerance, increased crown root growth, and the release of organic acids in rice (Frei et al., 2010). Zn accumulation in the root is also influenced by metal chelators like phytochelatins and metallothioneins, which bind Zn for transport (Palmgren et al., 2008). In Poaceae, Zn is absorbed as Zn–PS complex or the Zn–DMA complexes (Tolay et al., 2001) and may exist as free ionic form (Zn^{2+}) or bound to chelators in rice (Yoneyama et al., 2015). The Zn ion influx into endodermis cells is facilitated by *OsZIP1* transporter expressed at the root surface (Satoh-Nagasawa et al., 2012). Overexpression of *AtZIP1* in barley resulted in high Zn concentration in grains (S. A. Ramesh et al., 2004).

Cu is another essential element, acting as an enzyme cofactor involved in photosynthesis, and important cellular processes include respiration, cell wall biogenesis, cellular oxidative defense, transcription protein trafficking signaling pathways, and Fe utilization (Puig et al., 2007). Plants lacking Cu exhibit altered metabolic processes. del Pozo et al. (2010) found that members of ZIPs transporters, such as *ZIP2* and *ZIP4*, along with the COPT family transporters (*COPT1*, *COPT2*, *COPT3*, and *COPT4*) are involved in Cu uptake from the rhizosphere, with Cu deficiency upregulating these transporters in roots (Wintz et al., 2003). After absorption, Cu^{2+} ions are coupled to specific soluble Cu chaperones into the root system, which transport Cu to various cellular compartments or sequestered in vacuole/apoplast to avoid cytotoxicity (Migocka & Malas, 2018). Ionic or complexed forms of Cu are transported from roots to shoots, while YSL transporters facilitate Cu loading into the phloem and transport it as Cu-NA or with small proteins (Waters & Grusak, 2008). Cu remobilization and distribution from leaves to reproductive organs involve transporters like COPT6 and CCH (Garcia-Molina et al., 2013). Despite recent advances in understanding genes responsible for uptake and transport of micronutrients, many things still remain unknown, particularly regarding the transporters involved in micronutrient loading into seeds via the phloem. In Figure 2, a schematic overview of various transporters involved in transport of micronutrients from the soil to the aerial parts of the plant and through the roots.

9 | EFFORTS, ACCOMPLISHMENTS, AND FUTURE PROSPECTS IN BIOFORTIFICATION

Biofortification emerged as a promising strategy in the early 21 century for achieving nutritional food security and combating hidden hunger (Devaux et al., 2021). This approach provides higher micronutrient content in staple crops while maintaining high yields, ensuring adoption and consumption of the crops by target population (Praharaj et al., 2021). Today, malnutrition, the COVID-19 pandemic, and climate change together pose significant risk to millions of people, further intensifying the need for biofortified foods, which can help improve immunity to withstand the effects of future pandemic-like situation. To address the narrow genetic base of modern crops, biofortification efforts toward utilization of wild germplasm and landraces offer enhanced micronutrient content. The three largest initiatives currently underway to develop biofortified varieties for nutritional security are HarvestPlus, Biocassava Project, and Biofortified OFSP Project under the National Agricultural Research Organization (NARO) (Saltzman et al., 2017). Biofortified crops are developed and promoted across Uganda and other African countries through collaboration among various programs, including HarvestPlus, the Sweet Potato Action for Security and Health in Africa (SASHA), and Building Nutritious Food Baskets (BNFB), aiming to improve nutrition and food security. In India, the Indian Council of Agricultural Research (ICAR) launched the "Biofortification in Selected Crops for Nutritional Security" (BSCNS) platform, focusing on improving nutrient levels in cereals and millets (Sheoran et al., 2022). Such biofortification policies and strategies are important for building resilience in vulnerable populations, particularly during food crises caused by pandemics and natural disasters. Research has also focused on identifying the anti-nutritional factors that reduce the bioavailability of key nutrients in crops. For instance, phytic acid, which decreases the bioavailability of Fe and Zn (Samtiya et al., 2020). On the other hand, the transgenic approach significantly contributes to crops where genetic variation is limited. While genetically modified crops have been developed, their practical utility in agricultural fields and human diets remains minimal. For example, golden rice, enriched with vitamin A, was developed in 2005 and received approval in 2018 (H. Bouis, 2018). Major biofortification efforts target enhancing the content of Fe, Zn, carotene, and essential amino acids in crops. (Priyadarshi et al., 2018; Singh et al., 2017, 2018). Between 2009 and 2013, biofortified crops were developed and distributed following nutritional efficacy testing and the establishment of delivery strategies was completed. So far, over 140 biofortified varieties of 10 essential staple crops have been developed, benefiting more than 40 million low-income individuals in developing nations who lack access to a diverse diet in around 30 developing countries that lack access to a diverse diet (Mishra et al., 2022). Annually, several biofortified crop varieties are developed and adopted in countries such as Brazil, India, and China, contributing to enhanced nutritional security (H. E. Bouis & Saltzman, 2017). In eight different crops (rice, wheat, maize, finger millet, little millet, mustard, groundnut, and yam), India has introduced 17 biofortified varieties, with 1.5 to 3 times more nutrition content than conventional varieties. To achieve effective biofortification, focus should be on improving micronutrient bioavailability while increasing their concentration in crops. Biofortified crops provide higher micronutrient content, and it is crucial that these crops must be adopted and consumed by the target population (Praharaj et al., 2021). Certain vitamins, like vitamin E, D, and C, and compounds, like choline, niacine, and provitamin A, aid in the absorption of selenium, calcium, phosphorus, iron, zinc, methionine, and tryptophan (P. K. Gupta et al., 2021). However, anti-nutrients like phytate and polyphenols can reduce the bioavailability of micronutrients in crops (Ertop & Bektas, 2018; Nuss & Tanumihardjo, 2010). The insufficient salt iodization to combat iodine (I) deficiency pinpoints the need for further research into I uptake and mobilization in plants, which can be enhanced via plant breeding or genetic engineering (Gonzali et al., 2017). Various abiotic and biotic stresses impact the growth and productivity of crops, which significantly reduce grain yield (Jha & Warkentin, 2020). Such stresses significantly alter the nutritional profile of the seeds. Micronutrients, especially those with antioxidant properties or components of enzymes properties involved in various metabolic processes, protect cells from oxidative damage caused by ROS during environmental stresses (Prasad, 2020; Prasad et al., 2004). Increasing the concentration of Fe and Zn in cereals through biotechnological approaches has shown promise (Huertas et al., 2022), as has improving the bioavailability of micronutrients via genetic engineering, which allows precise gene manipulation, cloning, and expression of gene in host organisms. In recent years, interest has risen in using beneficial soil bacteria to enhance mineral uptake in crops, though its potential remains unexplored across various crops and it presents a new avenue for crop improvement (Singh & Prasanna, 2020). Advances in plant breeding and biotechnology can help to develop biofortified cultivars with important essential micronutrients in the era of climate change. Crop breeding for better nutritional traits is a long process that must include improvement in the bio-accessibility and bioavailability of Fe and Zn (S. B. Kumar et al., 2022; H. Kumar et al., 2019). Biotechnological tools, such as RNAi, have been utilized for biofortification in crop plant, such as enriching tomatoes with antioxidants (Niggeweg et al., 2004). Other attempts involve assimilation of essential elements like Zn, Mg, Cu, Se, Ca, Fe, I, S, P, and so on (Saurabh et al., 2014). Additionally, the recently evolved genome editing techniques, such as CRISPR-Cas9, allow for precise changes in genome (R. Kumar et al., 2021; Menz et al., 2020). Gene-editing approaches have proven particularly effective in biofortifying crops with CRISPR-Cas9 being an important tool for improvement (Hamdan et al., 2022; H. Kumar et al., 2019).

10 | CONCLUSION

Biofortification of crops has become a key focus for researchers, industries, and policymakers due to its potential to address global malnutrition. By enhancing the nutritional value of crops, biofortification offers a sustainable approach for improving the health of malnourished population worldwide. Tackling micronutrient deficiencies requires a multifaceted approach, including plant breeding, transgenic, and mineral fertilizer applications, all of which hold considerable potential. Achieving these goals necessitates collaboration among experts of diverse fields, including agronomists, plant breeders, biotechnologists, genetic engineers, and nutritionists, working together to develop sustainable and impactful solutions. One major challenge in biofortification is that nutrient assimilation is controlled by several genes, which regulate nutrient accumulation in roots, transport, and assimilation in the plants' shoots. Hormonal crosstalk plays a key role in modulating the expression of genes involved in nutrient/essential element transport. Additionally, gene pyramiding to target multiple nutrient traits is particularly challenging in breeding due to genetic complexity. Conventional breeding, molecular breeding, and transgenic approaches are commonly used for the biofortification of crops. In addition, multi-biofortification, which involves fortifying crops with several micronutrients, holds promise as a more effective approach than introducing multiple crops or cultivars enriched with a single nutrient. Also, via transgenic approach, only 2.4% of biofortified rice varieties are available for farmers and consumers, highlighting the strict regulatory barriers that limit their broader adoption. Development of multi-biofortified cultivars through transgenic approaches could provide a better combined nutrient coverage; however, regulatory approvals limit their usage. To promote the adoption and consumption of biofortified crops, tailored communication and marketing strategies that align with the ethical and economic context of target countries must be developed. Public support is also important for establishing policies and regulations that encourage acceptance of biofortified crops. Despite the challenges, biofortification holds tremendous potential for providing healthier food options to billions of people through sustainable practices. Likewise, creating mutants with fortified crops through genetic engineering would be a solution as they do not fall under transgenic regulatory rules. We believe the available efficient and precise genome editing tools will offer hope for overcoming these limitations. These innovations will make biofortification approaches more precise and effective, paving the way for a more sustainable and nutritious future.

AUTHOR CONTRIBUTIONS

Ashish Gautam: Conceptualization; investigation; methodology; writing—original draft; writing—review and editing. **Vinay Sharma**: Conceptualization; investigation; methodology; supervision; visualization; writing—original draft; writing—review and editing. **Charupriya Chauhan**: Writing—original draft; writing—review and editing. **Anamika Thakur**: Visualization; writing—original draft; writing—review and editing. **Manish K. Pandey**: Writing—review and editing. **Kagolla Priscilla**: Writing—review and

editing. **Rinku Dagar**: Writing—review and editing. **Xiaoli Jin**: Writing—review and editing. **Pawan Sukla**: Writing—review and editing. **Anirudh Kumar**: Writing—review and editing. **Rakesh Kumar**: Conceptualization; investigation; methodology; supervision; visualization; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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